THESIS

GRASSLAND PRODUCTIVITY IN THE COMMUNITY LAND MODEL: BIAS AND CLIMATE SENSTIVITY ACROSS NATIONAL ECOLOGICAL OBSERVATORY NETWORK SITES

Submitted by

Rachel Hallmark

Department of Ecosystem Science and Sustainability

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2026

Master's Committee:

Advisor: Danica Lombardozzi

Nathan Mueller
Melinda Smith
Nicholas Smith

ABSTRACT

GRASSLAND PRODUCTIVITY IN THE COMMUNITY LAND MODEL: BIAS AND CLIMATE SENSTIVITY ACROSS NATIONAL ECOLOGICAL OBSERVATORY NETWORK SITES

Grasslands are responsible for a large portion of terrestrial carbon fixation; therefore understanding how grasslands will respond to future global change is essential for predictions about the global carbon cycle. This study uses the Community Land Model (CLM) paired with the NCAR-NEON system at National Ecological Observatory Network sites to evaluate model bias and assess grassland productivity and plant functional type (PFT) responses to future environmental change scenarios including modified CO_2, drought, and warming. We found that CLM overestimates gross primary productivity (GPP) at sites classified as C_4 and C_3 arctic PFTs and slightly underestimates GPP at sites classified as the C_3 PFT. Across all PFTs grassland GPP significantly decreased in response to low CO_2 and showed a nonsignificant increase in response to high CO_2. We imposed two drought treatments of different duration, a year-long drought and a growing season drought and found that both treatments significantly decreased GPP across all PFTs, but the response to year-long drought was stronger. Simulated 2°C warming caused the most variable and smallest GPP response, with a significant decrease for the C_3 PFT, a significant increase for the C_3 arctic PFT, and no significant response for the C_4 PFT. These results highlight both the utility of the NCAR-NEON system for model evaluation and areas where CLM's representation of PFT-level grassland physiology could be improved.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

Terrestrial photosynthesis is the primary driver of land-atmosphere carbon exchange, with gross primary productivity (GPP) fixing roughly 123 petagrams of carbon from the atmosphere each year, making photosynthesis an important mechanism in offsetting anthropogenic carbon emissions (Beer et al., 2010; Friedlingstein et al., 2022). However, terrestrial carbon fixation is not a uniform process, and GPP can vary substantially by ecosystem, photosynthetic strategy, and climatic conditions (Beer et al., 2010). Grasslands are a large driver of this terrestrial carbon fixation as they cover about 40% of the Earth's surface (Blair et al., 2014), and combined grasslands and savannas account for about 33% of terrestrial GPP (Beer et al., 2010).

Grassland productivity is highly sensitive to climatic variability, with CO_2 concentration, drought, and temperature having a large impact on productivity (Ainsworth & Long, 2005; Wang et al., 2019). This sensitivity makes grasslands both vulnerable to future climate change and important for understanding future carbon cycling. Water availability is a large driver of grassland productivity and can be strongly variable from year to year (Moran et al., 2014). Future warming is also expected to influence future grassland productivity, although grasslands with differing photosynthetic strategies and baseline climatic conditions are predicted to have variable responses to warming (Havrilla et al., 2023; Wang et al., 2019). C_3 and C_4 grasses have different physiological strategies (Sage & Pearcy, 2000), therefore understanding how each will respond to climate change is essential for accurate predictions of future carbon cycling.

Most C_4 plants are grasses and dominate GPP in subtropical and semi-arid ecosystems (Still et al., 2003). Many important agricultural crops including maize, sugarcane, and sorghum utilize C_4 photosynthesis (Von Caemmerer et al., 2017). In total, C_4 plants account for roughly 20% of terrestrial GPP, even though they only make up about 5% of total plant species (Luo et al., 2024; Monson & Collatz, 2012). As opposed to the more common C_3 photosynthesis strategy, plants that use C_4 photosynthesis are typically more efficient at fixing carbon due to their ability to concentrate CO_2 around the CO_2 fixing enzyme, Rubisco (Sage & Pearcy, 2000). Rubisco has a high affinity for both carbon and oxygen, so this CO_2 concentrating mechanism minimizes Rubisco's reaction with oxygen which reduces photorespiration and allows more energy to be used for photosynthesis (Sage & Pearcy, 2000). Efficient use of CO_2 also allows C_4 plants to maintain high productivity while minimizing stomatal conductance, which can make them more water use efficient than C_3 plants (Sage & Pearcy, 2000). Differences in physiology between C_3 and C_4 plants suggest that grasslands dominated by each may respond differently to changing environmental conditions like drought, warming, and elevated CO_2, caused by climate change.

The carbon concentrating mechanism (CCM) in C_4 plants allows them to maintain high productivity in many conditions that limit C_3 photosynthesis, including low ambient CO_2, high temperatures, and water stress. In C_4 plants Rubisco saturates with CO_2 at ambient CO_2 levels of 200-300ppm (Sage & Pearcy, 2000), therefore C_4 plants show little productivity response to rising atmospheric CO_2, whereas C_3 plants experience fertilization from higher ambient CO_2 (Ainsworth & Long, 2005). Unlike the response to elevated CO_2, C_4 plants have an advantage over C_3 plants at higher temperatures because Rubisco's affinity for oxygen increases at high temperatures, so C_4 plants' ability to limit photorespiration via the CCM allows them to be more

productive than C_3 plants at higher temperatures (Ehleringer & Björkman, 1977; Sage & Kubien, 2007). By limiting stomatal conductance and thus reducing water loss while gaining CO_2, the CCM also gives C_4 plants a competitive advantage under mild drought as compared to C_3 plants (Samuel H. Taylor et al., 2014). These physiological phenomena are demonstrated in the evolution and ecology of C_4 plants. C_4 plants evolved under low ambient CO_2 and are presently most prominent in warm environments, while C_3 grasses are more common in cooler environments (Sage, 2004; Still et al., 2003). As climate change alters temperature, precipitation, and CO_2 simultaneously, the physiological responses of C_4 plants to these changes will significantly impact terrestrial carbon cycling.

The ecological and agricultural importance of grasslands makes understanding how they will respond to warming, drought, and changing CO_2 levels essential for predictions of global carbon cycling and food security. Earth system models (ESMs) are a valuable tool to predict how terrestrial vegetation will respond to global change. The Community Land Model (CLM), the land component of the Community Earth System model (CESM), separately represents C_3 and C_4 photosynthesis. While considerable recent work has contributed to the understanding of C_3 photosynthesis in ESMs (Rogers et al., 2017), the model used for C_4 photosynthesis in CLM was originally parameterized in single leaves of corn (Collatz et al., 1992) and to our knowledge its performance has not been evaluated in natural systems at the ecosystem scale.

This study uses CLM to evaluate the (Collatz et al., 1992) model of photosynthesis at National Ecological Observatory Network (NEON) grassland sites. Our aims are to 1) evaluate how CLM performs by comparing model GPP output to observed eddy covariance flux tower data from NEON and 2) impose environmental changes using CLM to assess whether C_3- and C_4-dominated grasslands as represented in CLM respond as expected by physiological principles

to altered CO_2, drought, and warming. These findings will inform efforts to improve the representation of grassland photosynthesis in ESMs, which is essential for understanding of how grassland productivity will change in response to climate change.

METHODS

Model Description

CLM simulates various fluxes between the land and atmosphere including fluxes of water, surface energy, nitrogen, and carbon (Lawrence et al., 2019). Simulations were run in CLM Version 5 using the NCAR-NEON system with Version 3 NEON forcing data. The NCAR-NEON system provides meteorological and ecological data from NEON sites, gap fills to have complete data, and uses the gap-filled data to simulate and evaluate CLM simulations, allowing for simulation outputs to be directly compared to NEON data (Lombardozzi et al., 2023). NEON measures ecosystem carbon fluxes using eddy covariance flux towers and GPP is derived from partitioned net ecosystem exchange measurements, whereas CLM simulates GPP using leaf-level photosynthesis scaled to the canopy (Lombardozzi et al., 2023). In the NCAR-NEON system vegetated land units are simulated as PFTs which are each given a unique set of parameters that are meant to emulate the physiological and ecological properties of that PFT. C_4 and C_3 grasses are represented as distinct PFTs and photosynthesis is calculated using the Collatz et al. (1992) and Farquhar et al. (1980) models of photosynthesis, respectively (Lawrence et al., 2018).

CLM simulations were run using satellite phenology (SP) mode. In SP simulations vegetation phenology and leaf area index (LAI) are prescribed using MODIS satellite data, rather

than being dynamically simulated (Lawrence et al., 2018). Additionally, SP mode does not simulate carbon-nitrogen cycling, therefore photosynthesis is not explicitly limited by nutrient availability (Cheng et al., 2021; Lawrence et al., 2018). Because phenology is prescribed from a climatological average based on satellite data, SP mode does not capture phenological responses to environmental change. However, the absence of nutrient-cycling, phenological changes, and dynamic LAI in SP mode ensures that GPP responds to our imposed environmental perturbations, making it useful for isolating leaf-level photosynthesis responses.

Site Selection

NEON sites are located across 20 various ecoclimatic regions in the United States, such that these field sites represent a diverse suite of environmental conditions ("About Field Sites and Domains | NSF NEON | Open Data to Understand our Ecosystems," n.d.). We ran simulations at all NEON sites that are classified as either a C_4, C_3 non-arctic, or C_3 arctic grass in CLM, excluding sites NIWO, MOAB, and CPER due to gaps in the meteorological forcing data. In total, we ran simulations at five C_4, four C_3 non-arctic, and two C_3 arctic grass sites. Selected sites span a wide range of geography and annual temperature and precipitation means, as shown in Table 1.

Table 1: Description of NEON field sites used for CLM simulations. Site name, Site ID, and coordinates columns are from NEON's field site descriptions ("Field Site Map and Info | NSF NEON | Open Data to Understand our Ecosystems," n.d.). Mean annual temperature (MAT) and mean annual precipitation (MAP) values are derived from CLM outputs and averaged across all simulation years. Plant functional type (PFT) descriptions follow the NCAR-NEON system described in Lombardozzi et al. (2023).

Site Name	Site ID	Coordinates	Mean annual precipitation (mm/year)	Mean annual temperature (°C)	CLM PFT
Utqiaġvik	BARR	71.2824, -156.6194	82.6	-9.0	C_3 arctic

Dakota Coteau Field Site	DCFS	47.16165, -99.10656	359.4	4.8	C_3 non-arctic
Disney Wilderness Preserve	DSNY	28.12505, -81.43619	1404.8	22.7	C_4
Healy	HEAL	63.8758, -149.2133	205.9	-0.7	C_3 arctic
Jornada Experimental Range	JORN	32.59069, -106.8425	136.3	17.1	C_4
Konza Prairie Biological Station	KONZ	39.10077, -96.56307	827.4	13.0	C_4
Lajas Experimental Station	LAJA	18.02126, -67.07689	997.5	25.4	C_4
Northern Great Plains Research Laboratory	NOGP	46.76972, -100.9154	228.6	6.0	C_3 non-arctic
Marvin Klemme Range Research Station	OAES	35.4106, -99.05878	979.1	15.9	C_4
San Joaquin Experimental Range	SJER	37.10878, -119.7323	785.9	18.4	C_3 non-arctic
Chase Lake National Wildlife Refuge	WOOD	47.1282, -99.24133	500.7	4.8	C_3 non-arctic

Simulation Setup

For each NEON site we began by running a default CLM-SP simulation, in which we changed no environmental variables, and simulations used the gap-filled meteorological forcing data from NEON. The NCAR-NEON system provides six years of meteorological forcing data from 2018-2023. To allow the model to equilibrate we ran simulations for a total of 18 years, cycling over the six years of forcing data three times. The first 12 years acted as a spin-up period, and the last six years were used for analysis. This approach emulates the spin-up process typically used in CLM biogeochemistry (BGC), however SP mode requires a shorter spin-up period because it does not simulate nutrient pools (Lawrence et al., 2018). In SP mode, gross

primary productivity fluxes stabilize by the 10th spin-up year, so our 12 year spin-up ensured stable fluxes prior to analysis (Lawrence et al., 2018).

Following the default simulations, we ran simulations with modified environmental conditions. Our imposed environmental perturbations included modified atmospheric CO_2 concentrations, drought scenarios, and warming. We only imposed one change per simulation, so that we were able to look at the photosynthetic response to one environmental change, as opposed to interactions of multiple environmental changes. Certain sites were excluded from some experiments due to challenges with the altering the forcing data. Detailed information on what site received what treatment is shown in Figure 1.

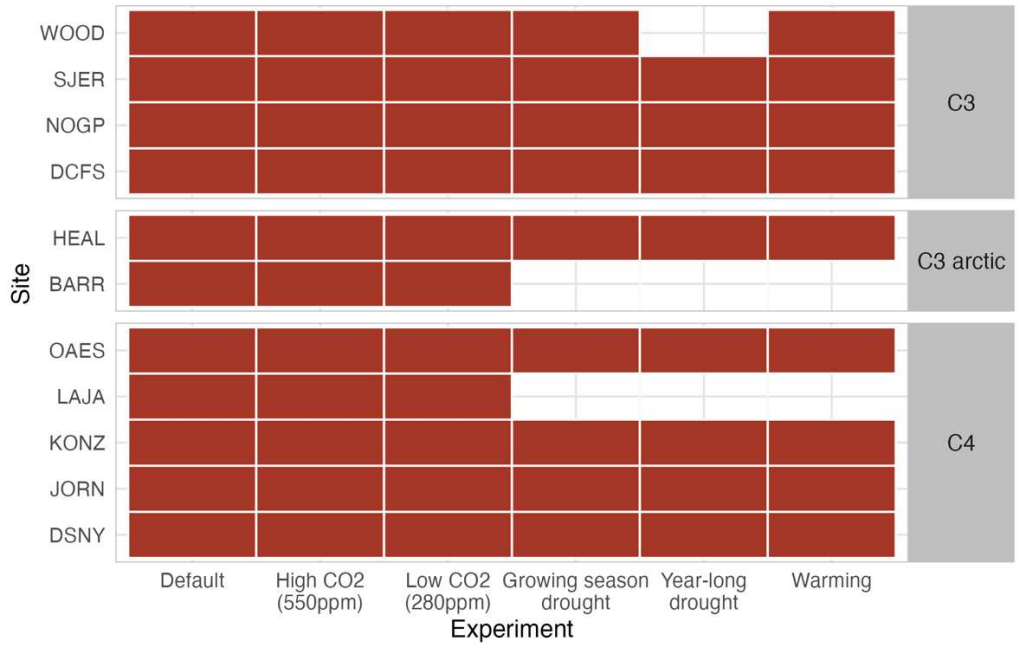

Figure 1: Grid of CLM simulation experiment and site combinations. Shaded areas indicate which site and experiment combinations were successfully run and included in our analysis.

Simulation Experiments

Modified CO_2

We ran simulation experiments with two different CO_2 scenarios. CO_2 concentration in default CLM simulations is set to 408 ppm. Our low CO_2 scenario, with CO_2 set to 280 ppm,

emulated pre-industrial CO_2 levels (Meinshausen et al., 2011). Our high CO_2 scenario had CO_2 set to 550 ppm to emulate free air CO_2 enrichment (FACE) field experiments that have been conducted in grasslands (Ainsworth & Long, 2005). Running model simulations with CO_2 set to a similar level as in field experiments allowed us to assess whether CLM reproduced the magnitude and direction of observed productivity responses to elevated CO_2.

Drought

For our experiments, we used the meteorological definition of drought, defined as a deficit in precipitation relative to long-term average conditions (Wilhite & Glantz, 1985). Grasses can have variable photosynthetic and productivity responses to drought depending on the severity and timing of drought (Carroll et al., 2021). Therefore, we imposed two different drought treatments to assess whether CLM responds as expected across a range of drought scenarios. We ran experiment simulations with two different drought treatments by altering precipitation regimens, reducing precipitation by 50% either 1) throughout all months of the simulation or 2) during the growing season only. Precipitation in default CLM simulations used NEON meteorological forcing data and we modified the precipitation variable in the meteorological forcing files while leaving everything else unchanged. Similar to manipulative experiments in grasslands, modifying precipitation in forcing files does not change vapor pressure or relative humidity.

To determine growing season, we used the R tidyverse and ncdf4 packages to analyze and plot default simulation output and determine the 4 months of the year with the highest simulated GPP at all sites (Pierce, 2010; Wickham et al., 2019). If the three of the four highest GPP months fell into the boreal meteorological summer (June, July, August (JJA)) as defined by the National Oceanic and Atmospheric Administration (NOAA), then we imposed drought

during those months ("Meteorological Versus Astronomical Seasons," 2016). Two sites, JORN and SJER, did not have three of their four high GPP months in JJA. Two of the highest months for JORN were July and August, but this site also exhibited high GPP in both late winter (February) and early fall (October). Because two of JORN's highest GPP months fell in JJA and the other high GPP months were not contiguous, we still used these summer months to impose growing season drought to maintain consistency with the treatment applied to most sites. SJER had its highest GPP months in late winter and spring (March, April, May) (Figure 2), so this was the only site that was treated as an exception because its highest GPP months did not overlap with JJA, warranting the imposed drought shift to spring.

Figure 2: Peak GPP months across NEON grassland sites. Darker boxes indicate the months with the 4 highest GPP values, lighter color boxes indicate the months with the 5th and 6th highest GPP values

Warming

We ran one warming experiment in which we increased temperature by 2ºC. Similar to precipitation, temperature in default simulations is determined by NEON meteorological data.

We followed the same methods used in our simulated precipitation experiment to edit model temperature inputs while leaving everything else unchanged. Warming by 2^{o}C is consistent with the SSP1-2.6 climate scenario (Intergovernmental Panel On Climate Change (Ipcc), 2023) and with mean warming magnitude from prior grassland studies (Wang et al., 2019). Imposing this temperature increase in our simulations allowed us to assess how grassland photosynthesis may respond to future warming.

Analysis

Daily output from CLM was given at 30-minute intervals for each site. Using the ncdf4 and tidyverse packages in Rstudio (Pierce, 2010; Wickham et al., 2019) we extracted photosynthesis, temperature, and precipitation data, averaged the 30-minute interval values into one daily value for analysis, and converted all units to a daily or monthly timescales. Analysis uses a combination of annual cycles and growing season averages to understand how grassland productivity changes throughout the year and interannual variability. We compare both absolute values to determine model bias and percent changes to understand relative responses to environmental perturbations.

To assess model bias, we compared difference in absolute GPP values between default CLM simulations and NEON observations by calculating the anomaly as *(default CLM – NEON).* For this comparison we calculated mean monthly GPP for each site across all simulation years, calculated the anomaly for each site, then grouped by PFT and took the average anomaly from the site level values. To understand model responses to environmental perturbations we calculated how much GPP in modified simulations changed in comparison to default as (*modified CLM – default CLM)/default CLM) * 100).* For our modified to default model comparison we filtered to only growing season months as defined in our drought experiment

methodology, as near-zero GPP values that occur during non-growing season months can cause large signals in percent change that may not be ecologically meaningful. In addition to the percent change analysis, we applied the Wilcoxon signed-rank test on mean annual growing season GPP at both the site and PFT level, comparing each site to itself and each PFT to itself, to assess whether treatments produced significantly different GPP from the default simulation.

RESULTS

Baseline NEON GPP

GPP observed from NEON eddy covariance flux towers followed a strong seasonal cycle at most sites, with GPP peaking during the summer and declining to near zero during winter months (Figure 3). On average, C_4 grass sites showed the highest peak GPP, reaching approximately 5 gC m^{-2} day^{-1} in June, followed by C_3 non-arctic grass sites, which peaked at approximately 4 gC m^{-2} day^{-1} in July. C_3 arctic sites showed a lower peak, reaching approximately 2.5 4 gC m^{-2} day^{-1} in July. Substantial variability existed among sites within a PFT with some C_4 and C_3 non-arctic sites reaching peak GPP as high as 9 and 6.5 gC m^{-2} day^{-1}, respectively, while one C_4 site had a peak GPP of less than 1 gC m^{-2} day^{-1} at its peak.

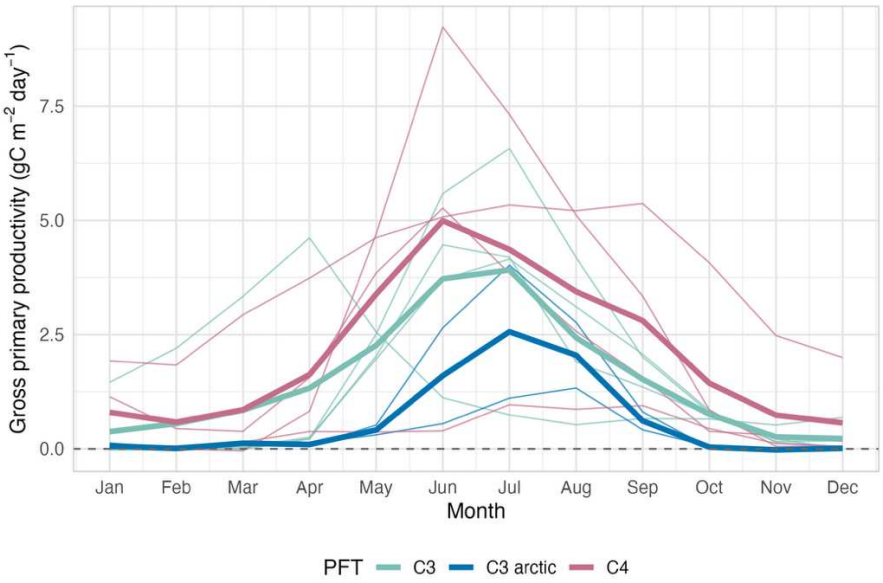

Figure 3: Annual cycle of gross primary productivity (GPP) from NEON observations for each grassland plant functional type (PFT). Thin lines represent the annual GPP cycle for individual sites and thick lines represent the average annual GPP cycle for each PFT. Note: "C3" in the legend refers to the C3 non-arctic PFT, distinct from C3 arctic.

NEON vs. CLM Comparison

CLM default simulations showed variable agreement with NEON observed GPP across PFTs (Figure 4). C_4 sites showed the largest positive anomaly of all PFTs evaluated, with CLM on average overestimating GPP by 3.15 gC m^{-2} day^{-1} at its peak in July. All C_4 sites had a positive GPP anomaly during the summer months (JJA), indicating that CLM consistently overestimates growing season GPP at C_4 sites, and the average anomaly is not being strongly skewed by any one site. CLM also overestimated summer GPP at C_3 arctic sites, though to a lesser degree than C_4 sites, with a peak positive GPP anomaly of 1.3 gC m^{-2} day^{-1} in July. C_3 non-arctic was the only PFT for which CLM did not overestimate summer GPP, with its largest negative GPP anomaly being 0.8 gC m^{-2} day^{-1} in June. However, there were two C_3 non-arctic sites where CLM overestimated GPP in the summer, suggesting that the anomaly pattern may not be as consistent in C_3 non-arctic sites as it is in C_4 and C_3 arctic sites.

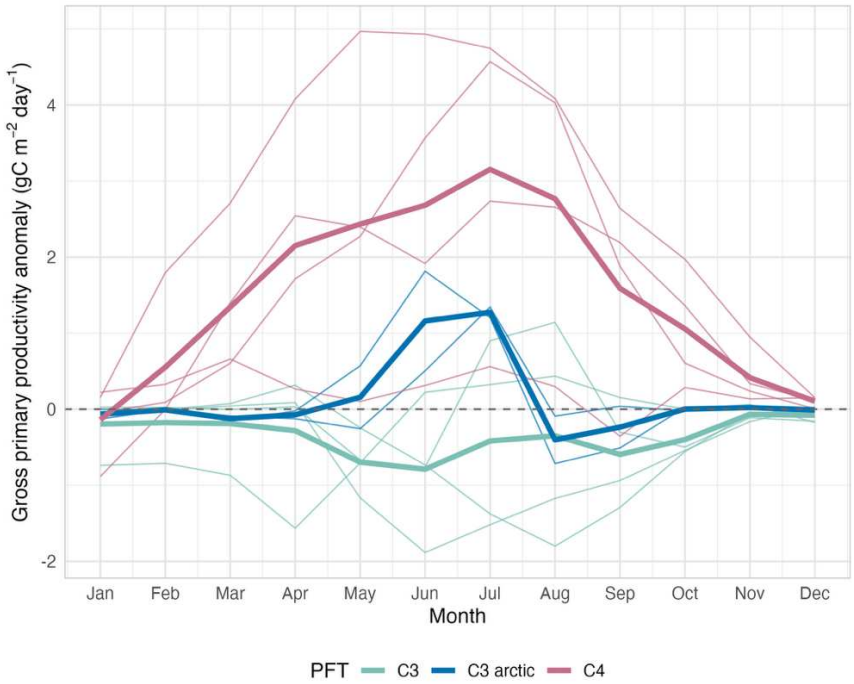

Figure 4: Annual cycle of gross primary productivity anomaly (CLM default – NEON observations) for each grassland plant functional type (PFT). Thin lines represent site level anomaly, and thick lines represent the mean PFT anomaly. Positive values indicate CLM simulates higher GPP than observations. Note: "C3" in the legend refers to the C3 non-arctic PFT, distinct from C3 arctic.

Simulation Experiments

Summary

GPP responses to CO_2 and drought treatments were consistent in direction across most sites and all PFTs, while responses to warming were more variable. Of all perturbations, the year-long drought treatment produced the largest magnitude response with a reduction in GPP. The growing season drought treatment also significantly decreased GPP across PFTs, but the magnitude of the decrease was much smaller than in the year-long drought treatment. While low CO_2 significantly decreased GPP across all PFTs, the slight increase in GPP seen in the high CO_2 treatment was small and not significant at the PFT level. Warming effects were not as consistent, with warming increasing GPP at C_3 arctic sites, decreasing GPP at C_3 non-arctic sites, and

causing no change to GPP at C_4 sites. These results are shown in Figure 5 and discussed in further detail below.

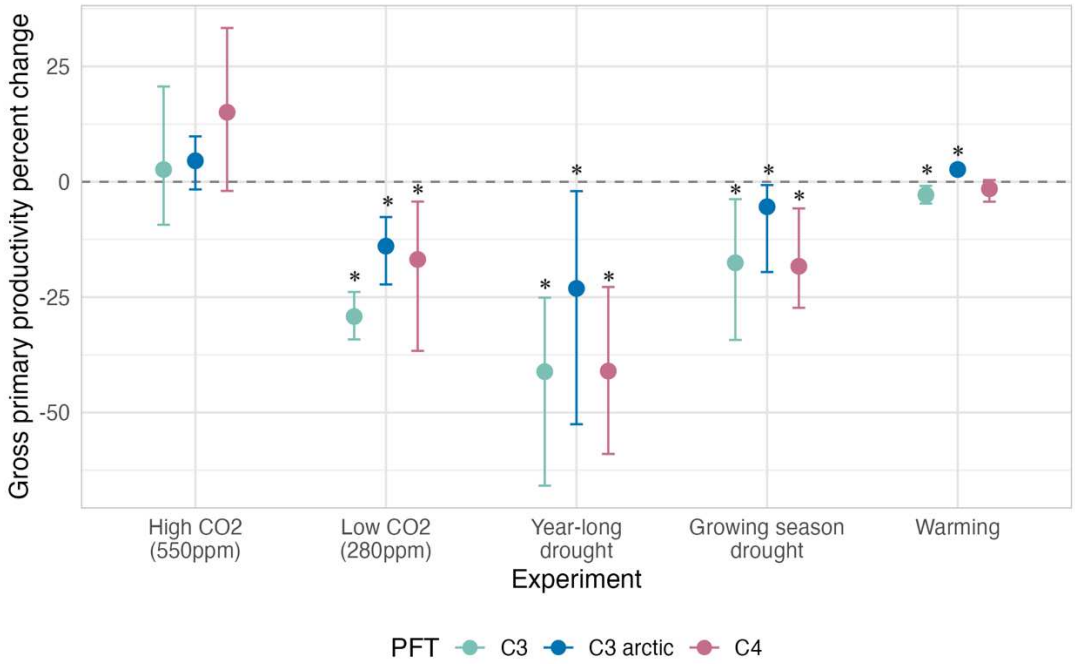

Figure 5: Gross primary productivity percent change from CLM default simulations by experiment across plant functional types. Points represent the mean percent change across all years, and error bars span the minimum and maximum percent change across all years. Asterisks (*) indicate treatment effects significantly different from zero ($p<0.05$). Note: "C3" in the legend refers to the C3 non-arctic PFT, distinct from C3 arctic.

Modified CO_2

There were similar patterns in response to each modified CO_2 treatment across all PFTs (Figure 6), with the low CO_2 treatment decreasing and the high CO_2 treatment increasing average growing season GPP. The low CO_2 treatment significantly decreased growing season GPP at all sites except SJER (C_3 non-arctic) and OAES (C_4). The high CO_2 treatment produced smaller and less consistent responses than the low CO_2 treatment, with significant increases in GPP only at two of four C_3 non-arctic sites, one of two C_3 arctic sites, and one of five C_4 sites. At the PFT

level the low CO_2 treatment significantly decreased GPP across all PFTs, while the high CO_2 treatment did not produce a significant response for any PFTs (Figure 5). At the PFT level, the decrease in C_3 non-arctic GPP was significantly larger than the decrease in C_3 arctic GPP. Notably, C_4 sites responded in the same direction to modified CO_2 as C_3 sites despite their theoretical insensitivity to changes in CO_2.

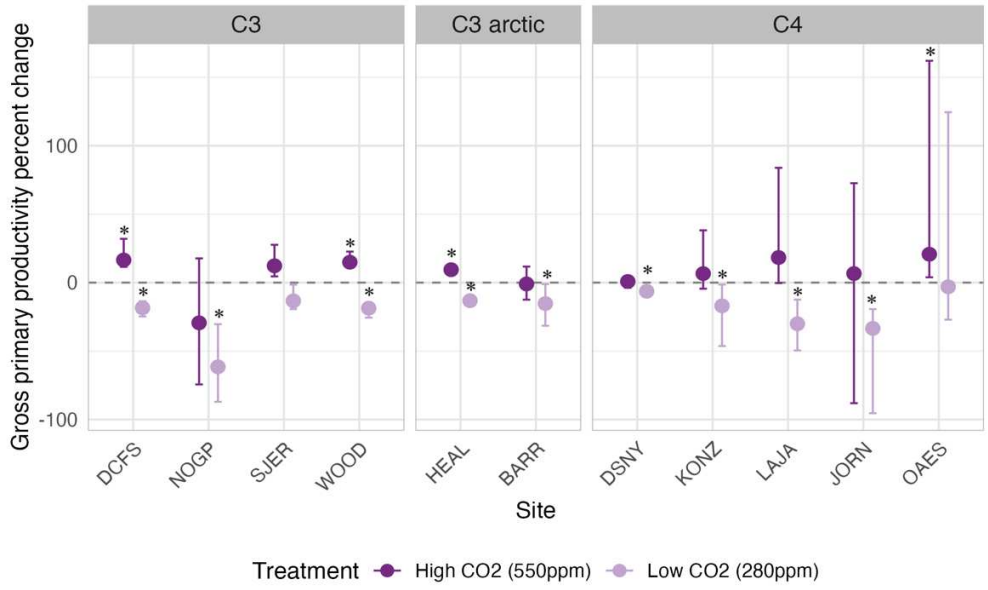

Figure 6: Gross primary productivity percent change from CLM default in modified CO_2 simulations at NEON grassland sites. Points, error bars, and asterisks are as in Figure 4. Note: "C3" in the panel label to the C3 non-arctic PFT, distinct from C3 arctic.

Drought

Both drought treatments, reduced precipitation during the growing season and reduced precipitation all year, caused a decrease in average growing season GPP at all sites (Figure 7). The growing season drought treatment consistently caused a smaller decrease in GPP than the year-long drought treatment, with the largest average site-level decrease in the year-long treatment being 67% at KONZ (C_4), while the largest average site-level decrease in the growing-season drought treatment was 51% at JORN (C_4). For the C_3 non-arctic and C_4 PFT, the year long drought produced a significantly larger response than the growing season drought. At sites where

the year-long drought significantly decreased GPP, the growing season drought also significantly decreased GPP. The only sites that did not have a significant decrease in GPP were SJER (C_3 non-arctic), WOOD (C_3 non-arctic), and DSNY (C_4). Interannual variability in GPP responses was high in sites across all PFTs, suggesting that GPP responses may be sensitive to variations in baseline precipitation regimes.

A consistent decrease in GPP in response to drought treatments was also seen across C_4, C_3 non-arctic, and C_3 arctic grass PFTs (Figure 5). At the PFT level C_3 non-arctic and C_4 grasses showed the largest GPP decrease in response to drought with mean reductions of about 41% and 18% for year-long and growing season drought respectively. Despite theoretical differences in drought tolerance, both drought treatments significantly decreased GPP for all PFTs.

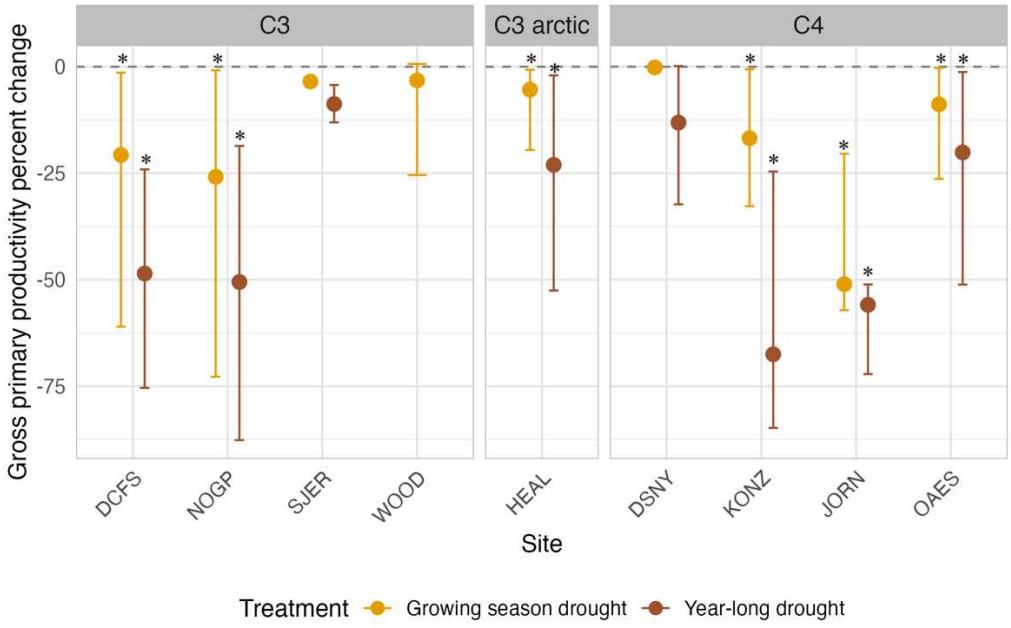

Figure 7: Gross primary productivity percent change from CLM default in drought simulations at NEON grassland sites. Points, error bars, and asterisks are as in Figure 4. Note: "C3" in the panel label to the C3 non-arctic PFT, distinct from C3 arctic.

Warming

Responses to warming across sites were not as consistent as responses to modified CO_2 and drought treatments. All C_3 non-arctic sites except SJER showed a significant decrease in GPP in response to warming, the C_3 arctic site showed a significant increase in GPP (Figure 8). C_4 sites had variable responses to warming with only JORN having a significant GPP response of -2.2%. At the PFT level warming significantly impacted GPP at C_3 non-arctic and C_3 arctic sites, but not at C_4 sites (Figure 5). GPP decreased by 2.8% at C_3 non-arctic sites and increased by 2.6% at C_3 arctic sites. GPP at C_4 sites did not change significantly in response to warming. At the PFT level, the response of C_3 arctic was significantly different than the response seen in both C_4 and C_3 non-arctic PFTs. The interannual variability at KONZ and OAES was large, with GPP increasing some years and decreasing other years, which likely contributed to the lack of significant response at the C_4 PFT level.

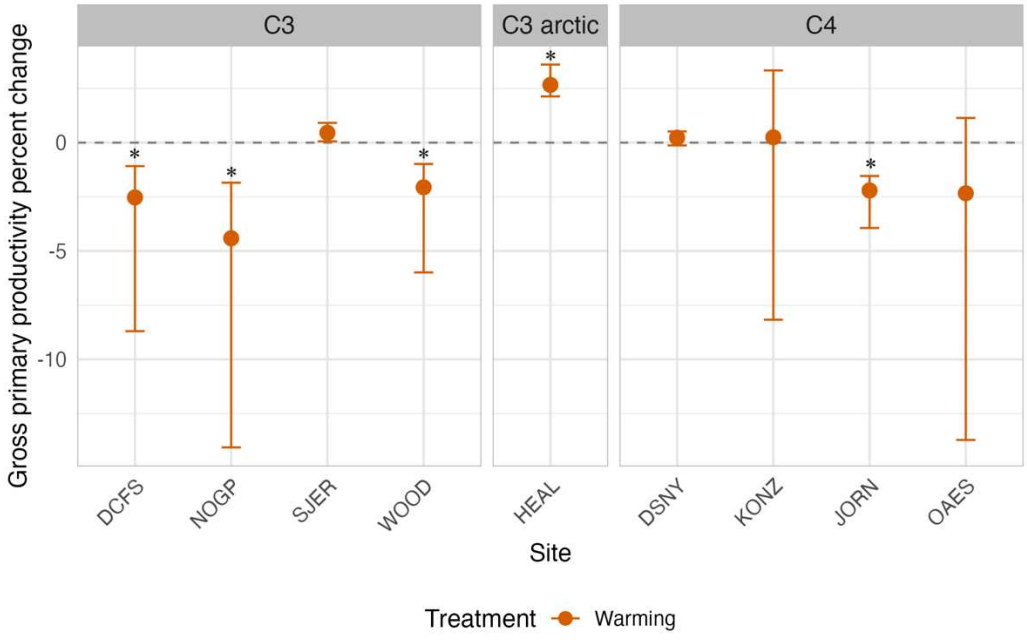

Figure 8: Gross primary productivity percent change from CLM default in warming simulations at NEON grassland sites. Points, error bars, and asterisks are as in Figure 4. Note: "C3" in the panel label to the C3 non-arctic PFT, distinct from C3 arctic.

DISCUSSION

Model Bias Evaluation

Accurate representation of grassland productivity in ESMs is important for understanding future global carbon cycling. Our work highlights existing biases in CLM's estimation of grassland GPP, with overestimation at all C_4 sites evaluated, slight overestimation at C_3 arctic sites, and slight underestimation at C_3 non-arctic sites. These findings are consistent with known biases in parameterization of photosynthetic capacity of C_4 grasses in CLM (Lawrence et al., 2019). Precipitation data quality in NEON forcing data may have contributed to GPP biases at some NEON grassland sites (Lombardozzi et al., 2023). Additionally, C_4 distribution studies show that none of the NEON sites we evaluated are entirely dominated by C_4 grasses (Still et al., 2003). If CLM assumes that baseline C_4 GPP is higher than C_3 GPP, and simulates sites as entirely C_4 even if they are more diverse, that could lead to an overestimation of GPP at NEON sites simulated as C_4 grasses. While GPP biases at C_3 arctic and C_3 non-arctic grass sites are worth highlighting, these biases are less consistent than those observed at C_4 sites. C_3 arctic grasses have limited representation in this study given the limited number of sites. At C_3 non-arctic sites the mean GPP bias was small, and two of the four sites evaluated did not exhibit a negative GPP bias during the growing season, suggesting that the negative GPP bias may not be a consistent feature of CLM across C_3 non-arctic grasslands.

Simulation Experiments

Modified CO_2

Beyond model bias, we also evaluated how simulated grassland productivity in CLM responds to modified CO_2. Across most sites and all PFTs, GPP tended to decrease with low CO_2. This was an expected result in the C_3 PFTs. C_3 plants do not have the same carbon concentrating mechanism as C_4 plants, and CO_2 saturation in C_3 plants typically occurs at concentrations well above ambient levels (Sage & Pearcy, 2000), meaning that our imposed treatment of 280ppm ambient CO_2 would make C_3 plants substantially carbon limited. However, the decrease in GPP under low CO_2 at C_4 sites was more unexpected. By concentrating CO_2 around Rubisco, C_4 plants are usually not CO_2 limited once ambient CO_2 concentrations reach about 200-300ppm (Sage & Pearcy, 2000), a range that our perturbation of 280ppm ambient CO_2 was well within. In CLM, C_3 and C_4 PFTs use the same stomatal conductance model, but with different parameters, that responds to ambient CO_2 (Lawrence et al., 2018), so it is possible that an increase in stomatal conductance caused by lower ambient CO_2 could have led to water loss and therefore limited GPP in C_4 plants, although further investigation would need to be done to evaluate this.

Similarly, across most sites and all PFTs, GPP slightly increased with higher ambient CO_2. While growing season GPP slightly increased for the C_3 PFTs, this response on average was not significant, which was unexpected given that C_3 plants have been well documented to increase productivity with increased CO_2 at both the plant (Poorter et al., 2022) and ecosystem scale (Ainsworth & Long, 2005). Because C_4 plants have been shown to saturate with CO_2 at 200-300ppm (Sage & Pearcy, 2000), it was also unexpected that the C_4 PFT exhibited CO_2 fertilization in CLM. While some FACE studies suggest that C_4 GPP does not respond strongly to elevated CO_2 (Ainsworth & Long, 2005), other studies have shown that this effect may be

reversed over long time periods (Reich et al., 2018) and that C_4 plants may not be as insensitive to high CO_2 as is typically thought (Wand et al., 1999). It is also worth noting that while we saw a slight increase in GPP in response to elevated CO_2, this response was not significant in any PFTs, whereas the response to low CO_2 was significant across all PFTs, suggesting that grassland productivity in CLM may be insensitive to small increases in CO_2, and more sensitive to decreases in CO_2.

Drought

Both imposed drought treatments significantly reduced GPP across most sites and all PFTs, consistent with previous work showing that drought can reduce grassland productivity (Moran et al., 2014). The year-long drought treatment consistently decreased GPP more than the growing season drought treatment. This response was consistent with findings that grasslands respond differently to drought of varying duration and intensity (Carroll et al., 2021; Wei et al., 2022). Every site that had a significant decrease in GPP in the year-long treatment also showed a significant decrease in GPP in the growing season treatment. The only sites that did not significantly respond to either drought treatment were those classified as sub-humid (mean annual precipitation between 500-800 mm/year) and humid (mean annual precipitation greater than 800 mm/year). Consistent with prior work on regional grassland responses to drought (Carroll et al., 2021; Knapp et al., 2001), this pattern in drought response and the large interannual variability in treatment response across years suggests that grassland responses to drought are highly dependent on site-specific precipitation regimes.

All PFTs showed a significant decrease in GPP in response to both drought treatments, but the magnitude of the response differed across PFTs. C_3 non-arctic and C_4 grasses showed similar responses to both drought treatments. Prior work has shown that C_3 grasses are typically

more sensitive to drought than C_4 grasses (Ripley et al., 2010; S. H. Taylor et al., 2011), which is not consistent with the response we observed from imposing drought in CLM. The response of C_4 grasses to drought was surprising given that C_4 plants should be able to maintain high photosynthesis under water limitation due to their carbon concentrating mechanism (Sage & Pearcy, 2000). However, it has also been found that while C_4 grasses can maintain their photosynthetic advantage under mild drought, this advantage may diminish under severe and prolonged drought (Ripley et al., 2010), which could explain the large decrease in C_4 GPP under the year-long compared to the growing season drought treatment. The C_4 PFT had a similar response to drought as the C_3 non-arctic PFT, suggesting that CLM may not be capturing expected physiological differences between these two pathways. This may stem from the shared stomatal conductance model, which, despite using different parameters (g_1) to control stomatal sensitivity to vapor pressure deficit for each PFT, may not explicitly represent the dry-tolerance associated with the CCM in C4 plants. However, it is also possible that C_4 grasses at sites that responded to drought were already operating at the edge of their dry-tolerance, so imposing drought could have pushed them past their limit of dry-tolerance and caused a decrease in GPP.

Warming

Of all simulation modifications, warming showed the most variable responses across sites and PFTs. The most consistent GPP response was seen at the C_3 non-arctic and C_3 arctic PFTs, with a significant decrease and increase in GPP respectively. The responses seen for C_3 non-arctic grasses are consistent with prior work that suggests C_3 grasses have a lower temperature optimum than C_4 grasses (Sage & Kubien, 2007), meaning that a 2°C warming could push C_3 plants past their optimal temperature. Additionally, increasing temperature without a subsequent increase in water availability could have caused water stress that limited GPP. Despite using the

C_3 photosynthesis pathway, the single C_3 arctic site analyzed showed an increase in GPP in response to warming. This is likely because at cold sites temperature can be a strong limitation to photosynthesis (Wang et al., 2019), so imposing a warming treatment allowed GPP to increase.

Unlike the C_3 non-arctic and C_3 arctic sites, C_4 sites showed much more variable responses to warming. Only one site had a significant response, with GPP decreasing at JORN. Two other sites (KONZ and OAES) had large interannual variability with an increase in GPP some years, and a decrease in other years. The site where GPP decreased had the highest average temperature (17°C) and lowest annual precipitation (136 mm/year) of all C_4 sites. These climatic conditions can help explain the responses to warming seen at this site. Prior work has found that C_4 grasses may increase productivity in cooler regions, but decline in productivity in hot and dry regions under future climate change (Havrilla et al., 2023). Physiological studies have suggested that C_4 plants may experience increased productivity in response to warming due to their higher temperature optimum (Sage & Kubien, 2007). CLM includes temperature acclimation for C_3 photosynthesis, allowing the optimal temperature to shift based on a 10-day running mean, however, CLM does not include this response for the C_4 photosynthesis (Lawrence et al., 2018). This may limit CLM's ability to capture the full productivity response of C_4 plants under warming.

CONCLUSION

This work used the Community Land Model to evaluate grassland productivity responses to future change scenarios including modified CO_2, drought, and warming. By using CLM paired

with the NCAR-NEON system to run simulations at NEON sites, we were able to compare CLM's simulated GPP to eddy covariance flux tower data to evaluate model bias and assess how CLM represents grassland response to simulated environmental change. We found that CLM generally overestimated GPP at C_4 and C_3 arctic grasslands, and slightly underestimated GPP at C_3 non-arctic grasslands. Grassland GPP generally increased in response to simulated high CO_2 and decreased in response to simulated low CO_2, although responses to high CO_2 were small and nonsignificant. We imposed two drought treatments of varying duration, a year-long and growing season drought, and found that both treatments reduced GPP for all PFTs, with the year-long drought treatment causing a larger decrease in GPP than the growing season treatment. Productivity response to warming was variable, with warming decreasing GPP at most C_3 non-arctic sites, increasing GPP at C_3 arctic sites, and causing variable GPP responses at C_4 sites.

CLM captures the general direction of expected grassland GPP response to environmental change, but may have limitations at the PFT level. C_4 grasses are expected to respond differently than C_3 grasses to future change due to their carbon concentrating mechanism that increases CO_2 and water use efficiency, and allows for a higher optimal temperature for photosynthesis. Across most experiments, productivity at C_4 sites responded in the same direction as C_3 non-arctic sites, though often with smaller magnitude. While we saw small differences in PFT level responses across treatments, CLM may not be accurately representing the differences between C_3 and C_4 physiology due to the unified stomatal conductance model and lack of temperature acclimation in C_4 plants. Given that default CLM simulations overestimated GPP at C_4 sites, and C_3 and C_4 sites responded similarly to environmental change, future work could involve testing different C_4 photosynthesis models in CLM to improve baseline simulations and tuning model parameters to distinguish differences in C_4 and C_3 physiology, phenology, and nutrient allocation.

While these findings hopefully will provide insight into directions for future model improvement and development, several limitations of this study provide room for future work. The NCAR-NEON system is a valuable tool for evaluating model outputs against observational data, however limited site options and issues with meteorological forcing data only allowed for a small number of sites to be evaluated, and precipitation biases may have influenced apparent model bias at some sites. Additionally, due to biases in leaf area index (LAI) outputs when running simulations with prognostic phenology, we chose to use satellite phenology mode for this study since photosynthesis is driven by LAI. However, to ensure accurate LAI is being used, it could be beneficial to use NEON phenocam LAI data. While SP mode provided a valuable way to isolate leaf-level photosynthetic responses without impacts of downstream nutrient cycling, because phenology and LAI are prescribed from satellite data, phenological and LAI responses to environmental change and were not captured. For example, LAI would likely change with CO_2 and drought, and those changes were not reflected here. Despite these limitations, this study demonstrates the value of the NCAR-NEON system as a tool for model evaluation and experimentation, and highlights areas where CLM's representation of grassland productivity could be improved to better understand grassland responses to future global change.

REFERENCES

About Field Sites and Domains | NSF NEON | Open Data to Understand our Ecosystems. (n.d.). Retrieved May 1, 2026, from https://www.neonscience.org/field-sites/about-field-sites

Ainsworth, E. A., & Long, S. P. (2005). What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. *New Phytologist*, *165*(2), 351–372. https://doi.org/10.1111/j.1469-8137.2004.01224.x

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., et al. (2010). Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate. *Science*, *329*(5993), 834–838. https://doi.org/10.1126/science.1184984

Blair, J., Nippert, J., & Briggs, J. (2014). Grassland Ecology. In Russell K. Monson (Ed.), *Ecology and the Environment* (pp. 389–423). New York, NY: Springer New York. https://doi.org/10.1007/978-1-4614-7501-9_14

Carroll, C. J. W., Slette, I. J., Griffin-Nolan, R. J., Baur, L. E., Hoffman, A. M., Denton, E. M., et al. (2021). Is a drought a drought in grasslands? Productivity responses to different types of drought. *Oecologia*, *197*(4), 1017–1026. https://doi.org/10.1007/s00442-020-04793-8

Cheng, Y., Huang, M., Zhu, B., Bisht, G., Zhou, T., Liu, Y., et al. (2021). Validation of the Community Land Model Version 5 Over the Contiguous United States (CONUS) Using In Situ and Remote Sensing Data Sets. *Journal of Geophysical Research: Atmospheres*, *126*(5), e2020JD033539. https://doi.org/10.1029/2020JD033539

Collatz, G., Ribas-Carbo, M., & Berry, J. (1992). Coupled Photosynthesis-Stomatal Conductance Model for Leaves of C4 Plants. *Functional Plant Biology*, *19*, 519–538. https://doi.org/10.1071/PP9920519

Ehleringer, J., & Björkman, O. (1977). Quantum Yields for CO_2 Uptake in C_3 and C_4 Plants: Dependence on Temperature, CO_2 , and O_2 Concentration. *Plant Physiology*, *59*(1), 86–90. https://doi.org/10.1104/pp.59.1.86

Farquhar, G. D., Von Caemmerer, S., & Berry, J. A. (1980). A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. *Planta*, *149*(1), 78–90. https://doi.org/10.1007/BF00386231

Field Site Map and Info | NSF NEON | Open Data to Understand our Ecosystems. (n.d.). Retrieved May 1, 2026, from https://www.neonscience.org/field-site-map-and-info

Friedlingstein, P., Jones, M. W., O'Sullivan, M., Andrew, R. M., Bakker, D. C. E., Hauck, J., et al. (2022). Global Carbon Budget 2021. *Earth System Science Data*, *14*(4), 1917–2005. https://doi.org/10.5194/essd-14-1917-2022

Havrilla, C. A., Bradford, J. B., Yackulic, C. B., & Munson, S. M. (2023). Divergent climate impacts on C_3 versus C_4 grasses imply widespread 21st century shifts in grassland functional composition. *Diversity and Distributions*, *29*(3), 379–394. https://doi.org/10.1111/ddi.13669

Intergovernmental Panel On Climate Change (Ipcc). (2023). *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of*

the Intergovernmental Panel on Climate Change (1st ed.). Cambridge University Press. https://doi.org/10.1017/9781009157896

Knapp, A. K., Briggs, J. M., & Koelliker, J. K. (2001). Frequency and Extent of Water Limitation to Primary Production in a Mesic Temperate Grassland. *Ecosystems*, *4*(1), 19–28. https://doi.org/10.1007/s100210000057

Lawrence, D. M., Fisher, R., Koven, C., & Oleson, K. W. (2018). *Technical Description of Version 5.0 of the Community Land Model* (National Center for Atmospheric Research No. NCAR/TN-560+STR). Boulder, Colorado.

Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., et al. (2019). The Community Land Model Version 5: Description of New Features, Benchmarking, and Impact of Forcing Uncertainty. *Journal of Advances in Modeling Earth Systems*, *11*(12), 4245–4287. https://doi.org/10.1029/2018MS001583

Lombardozzi, D. L., Wieder, W. R., Sobhani, N., Bonan, G. B., Durden, D., Lenz, D., et al. (2023). Overcoming barriers to enable convergence research by integrating ecological and climate sciences: the NCAR–NEON system Version 1. *Geoscientific Model Development*, *16*(20), 5979–6000. https://doi.org/10.5194/gmd-16-5979-2023

Luo, X., Zhou, H., Satriawan, T. W., Tian, J., Zhao, R., Keenan, T. F., et al. (2024). Mapping the global distribution of C4 vegetation using observations and optimality theory. *Nature Communications*, *15*(1), 1219. https://doi.org/10.1038/s41467-024-45606-3

Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J.-F., et al. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change*, *109*(1–2), 213–241. https://doi.org/10.1007/s10584-011-0156-z

Meteorological Versus Astronomical Seasons. (2016, March 10). Retrieved May 1, 2026, from https://www.ncei.noaa.gov/news/meteorological-versus-astronomical-seasons

Monson, R.K., & Collatz, G. J. (2012). The ecophysiology and global biology of C_4 photosynthesis. In J. Flexas, F. Loreto, & H. Medrano (Eds.), *Terrestrial Photosynthesis in a Changing Environment* (1st ed., pp. 54–70). Cambridge University Press. https://doi.org/10.1017/CBO9781139051477.007

Moran, M. S., Ponce-Campos, G. E., Huete, A., McClaran, M. P., Zhang, Y., Hamerlynck, E. P., et al. (2014). Functional response of U.S. grasslands to the early 21st-century drought. *Ecology*, *95*(8), 2121–2133. https://doi.org/10.1890/13-1687.1

Pierce, D. (2010). ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files [Data set]. https://doi.org/10.32614/CRAN.package.ncdf4

Poorter, H., Knopf, O., Wright, I. J., Temme, A. A., Hogewoning, S. W., Graf, A., et al. (2022). A meta-analysis of responses of C3 plants to atmospheric CO2: dose–response curves for 85 traits ranging from the molecular to the whole-plant level. *New Phytologist*, *233*(4), 1560–1596. https://doi.org/10.1111/nph.17802

Reich, P. B., Hobbie, S. E., Lee, T. D., & Pastore, M. A. (2018). Unexpected reversal of C3 versus C4 grass response to elevated CO2 during a 20-year field experiment. *Science*, *360*(6386), 317–320. https://doi.org/10.1126/science.aas9313

Ripley, B., Frole, K., & Gilbert, M. (2010). Differences in drought sensitivities and photosynthetic limitations between co-occurring C3 and C4 (NADP-ME) Panicoid grasses. *Annals of Botany*, *105*(3), 493–503. https://doi.org/10.1093/aob/mcp307

Rogers, A., Medlyn, B. E., Dukes, J. S., Bonan, G., von Caemmerer, S., Dietze, M. C., et al. (2017). A roadmap for improving the representation of photosynthesis in Earth system models. *New Phytologist*, *213*(1), 22–42. https://doi.org/10.1111/nph.14283

Sage, R. F. (2004). The evolution of C_4 photosynthesis. *New Phytologist*, *161*(2), 341–370. https://doi.org/10.1111/j.1469-8137.2004.00974.x

Sage, R. F., & Kubien, D. S. (2007). The temperature response of C_3 and C_4 photosynthesis. *Plant, Cell & Environment*, *30*(9), 1086–1106. https://doi.org/10.1111/j.1365-3040.2007.01682.x

Sage, R. F., & Pearcy, R. W. (2000). The Physiological Ecology of C4 Photosynthesis. In R. C. Leegood, T. D. Sharkey, & S. von Caemmerer (Eds.), *Photosynthesis: Physiology and Metabolism* (pp. 497–532). Dordrecht: Springer Netherlands. https://doi.org/10.1007/0-306-48137-5_21

Still, C. J., Berry, J. A., Collatz, G. J., & DeFries, R. S. (2003). Global distribution of C_3 and C_4 vegetation: Carbon cycle implications. *Global Biogeochemical Cycles*, *17*(1). https://doi.org/10.1029/2001GB001807

Taylor, S. H., Ripley, B. S., Woodward, F. I., & Osborne, C. P. (2011). Drought limitation of photosynthesis differs between C_3 and C_4 grass species in a comparative experiment. *Plant, Cell & Environment*, *34*(1), 65–75. https://doi.org/10.1111/j.1365-3040.2010.02226.x

Taylor, Samuel H., Ripley, B. S., Martin, T., De-Wet, L., Woodward, F. I., & Osborne, C. P. (2014). Physiological advantages of C_4 grasses in the field: a comparative experiment demonstrating the importance of drought. *Global Change Biology*, *20*(6), 1992–2003. https://doi.org/10.1111/gcb.12498

Von Caemmerer, S., Ghannoum, O., & Furbank, R. T. (2017). C_4 photosynthesis: 50 years of discovery and innovation. *Journal of Experimental Botany*, *68*(2), 97–102. https://doi.org/10.1093/jxb/erw491

Wand, S. J. E., Midgley, GuY. F., Jones, M. H., & Curtis, P. S. (1999). Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology*, *5*(6), 723–741. https://doi.org/10.1046/j.1365-2486.1999.00265.x

Wang, N., Quesada, B., Xia, L., Butterbach-Bahl, K., Goodale, C. L., & Kiese, R. (2019). Effects of climate warming on carbon fluxes in grasslands— A global meta-analysis. *Global Change Biology*, *25*(5), 1839–1851. https://doi.org/10.1111/gcb.14603

Wei, X., He, W., Zhou, Y., Ju, W., Xiao, J., Li, X., et al. (2022). Global assessment of lagged and cumulative effects of drought on grassland gross primary production. *Ecological Indicators*, *136*, 108646. https://doi.org/10.1016/j.ecolind.2022.108646

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., et al. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686.

Wilhite, D. A., & Glantz, M. H. (1985). Understanding: the Drought Phenomenon: The Role of Definitions. *Water International*, *10*(3), 111–120. https://doi.org/10.1080/02508068508686328